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Growth and development rates in a riparian spider are altered by asynchrony between the timing and amount of a resource subsidy

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Abstract Rapid growth in response to increased prey abundance may be induced by environmental variability associated with resource subsidies. Spiders living in riparian areas are subject to frequent, episodic bursts of aquatic prey (subsidies). These periods of high resource abundance may occur at different points in recipient consumers' development through variation in emergence patterns of prey between years or across a landscape. We examine how variable timing of subsidy abundance intersects with life history scheduling to produce different growth and development outcomes for individuals within a population. Through a series of controlled feeding experiments, we tested the hypotheses that the spider *Tetragnatha versicolor*: (1) exhibits compensatory growth in response to subsidy variability, (2) that rapid increases in mass may result in a greater risk of mortality, and (3) that the timing of subsidy resources relative to the development schedule of this spider may produce different outcomes for individual growth patterns and adult condition. Spiders fed at very high rates grew fastest but also showed evidence of increased mortality risk during moulting. *T. versicolor* is capable of exhibiting strong growth compensation—individuals suffering initial growth restriction were able to catch up completely with animals on a constant diet utilising the same amount of food. Spiders that received an early pulse of resources (simulating an early arrival of an aquatic insect subsidy to riparian forests) did worse on all measures of development and fitness than spiders that received either a constant supply of food or a late pulse of resources. Importantly, receiving large amounts of food early in life appears to actually confer relative disadvantages in terms of later performance compared with receiving subsidies later in development. Subsidies may provide greater benefits to individuals or age cohorts encountering this resource abundance closer to the onset of reproductive efforts than subsidies arriving early in development.

Keywords Aquatic–terrestrial interactions · Subsidy timing · Compensatory growth · Life history phenology · *Tetragnatha versicolor*

Introduction

There is strong evidence from a growing number of ecological systems that dynamics of local populations can be altered by short-duration pulses of resource subsidies from adjacent habitats. These temporally and spatially variable pulses of prey and nutrients have garnered significant attention from ecologists in recent years (e.g. Briers et al. 2005; Gende and Willson 2001; Mendelssohn and Kuhn 2003; Orr et al. 2005; Szepanski et al. 1999). However, there have been few studies of the ultimate consequences of this temporal variability in resource subsidies for the fitness of recipient organisms (but see Baxter et al. 2007; Sabo and Power 2002). While many of these resource flows are strongly seasonal—as in the summer emergence of aquatic insects—the timing of their arrival *within* a season may also have implications for organisms that show growth plasticity or experience constraints and thresholds related to life history phenologies.

The idea of a subsidy contains the notion that these resources are of benefit to consumer populations (Polis

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et al. 1997). Indeed, most investigations have focused on the effects of subsidies at the level of whole populations. For example, Sabo and Power (2002) determined that algal subsidies increased the overall density of riparian lizards, while Polis and Hurd (1996) reported that larger total populations of web-building spiders occurred on islands with birds (via subsidies of both sea wrack and guano). However, within a population, individuals will have variable access to subsidies and not all individuals will respond to subsidies in the same fashion. Allochthonous resources that arrive patchily in both space and time may be encountered by some portion of the population with greater frequency than others, particularly when a population is size structured, has overlapping generations or shows habitat separation between age classes.

In order for subsidies to be of benefit, an individual organism needs to be able to take advantage of them when they are present. One necessary condition for this to occur is for an organism to be flexible in its growth strategy and to capitalize on sudden abundances of resources by growing rapidly when it can. Organisms may show accelerated growth following periods of relative food shortage, which can exceed that normally observed on the same ration (Jespersen and Toft 2003; Metcalfe and Monaghan 2001). Periods of rapid growth may be induced by environmental variation in food supply and may carry inherent ecological and physiological risks as well as clear benefits (Fischer et al. 2004). Ecological costs include an increased exposure to predators and parasites during increased foraging (Abrams et al. 1996). Increasingly, researchers have demonstrated that there may also be intrinsic physiological costs associated with these periods of rapid growth including a decreased resistance to starvation and other environmental stresses (Fischer et al. 2004; Metcalfe and Monaghan 2001; Yearsley et al. 2004), or an increased risk of mortality during life history transitions (Higgins and Rankin 2001). These costs of rapid growth may be traded off against the potential for organisms to catch up to or exceed the size attained by conspecifics that did not experience a resource restriction (Yearsley et al. 2004).

Many spiders have been shown to have a combination of very low metabolic rates and a capacity to opportunistically ingest large amounts of prey (Foelix 1996). Orb-weaving spiders are generally assumed to be sit-and-wait predators that gorge when prey are abundant. This strategy should result in occasional periods of very rapid increases in mass. Spiders living in strongly seasonal environments, where synchronized aquatic insect emergence results in alternate episodes of prey availability and food limitation, may thus be particularly vulnerable to costs associated with rapid growth or delayed costs of compensatory growth due to variability in this resource subsidy encountered during different stages of spider development or by different age classes within a population.

Although riparian spiders have been the subject of studies of changes in population level distribution or abundance in response to subsidies (Kato et al. 2003; Marczak and Richardson 2007; Polis and Hurd 1995), the impact of aquatic insect subsidies on individual growth or condition has yet to be examined. The long-jawed orb weaver *Tetragnatha versicolor* Walckenaer 1842 (Araneae: Tetragnathidae) can capitalize on subsidy resources at any time of the year since it is active throughout the year. However, its non-synchronous life cycle (L. B. Marczak, unpublished data) means that there are individuals of many different ages present at any given time. We tested the ability of *T. versicolor* to exhibit both plastic growth as a general response to a variable food environment and its ability to compensate for early nutritional shortages. We then compared the effect of large food pulses (for instance, the highly episodic subsidy of emerging aquatic insects) received early in development (early rapid growth) versus subsidies received just prior to the penultimate molt (later compensatory growth). We conducted three laboratory experiments in which juvenile *T. versicolor* spiders were randomly assigned to treatments in which we varied total food availability quantitatively and temporally. We address the following questions:

1. Is there a detectable increase in mortality risk associated with rapid growth?
2. Is *T. versicolor* capable of compensatory growth responses?
3. How does the variable timing of subsidy abundance intersect with tradeoffs in the individual fitness consequences of rapid or compensatory growth?

Materials and methods

Study organism

The orb-weaving spider *Tetragnatha versicolor* is a broadly distributed species with a consistent association with freshwater habitats, largely feeding on emerging aquatic insects (Williams et al. 1995). Although aquatic insects emerge throughout the year in the region where this study was conducted, peaks in emergence occur at different times from different streams (J. Richardson, unpublished data). In coastal British Columbia, this spider has an adult body size between 6 and 10 mm (tibia–patella length; TPL) and has a mainly annual life cycle with non-synchronous age classes producing overlapping adults and juveniles during the summer reproductive period (L. Marczak, unpublished data).

For our experiments we used either wild-caught juveniles (experiment 1: variable growth and mortality risk) or laboratory-reared individuals from wild-collected females (22 spiderlings from three wild-caught females for compensatory growth experiment, 70 spiderlings from ten wild-caught females for timing of subsidy experiment). Wild-collected spiders were hand-picked from webs adjacent to small headwater streams in Malcolm Knapp Research Forest (49°18′40″N, 122°32′40″W), in coastal British Columbia, between May and June 2005 and in June 2006. Wild-collected, visibly gravid female spiders were kept for 1 week in the lab at an average temperature of 21°C until an egg case was laid. Lab-reared spiders were maintained on an ad libitum diet of local honeybee pollen and *Drosophila melanogaster* reared in a medium enriched with crushed, high protein dog food (Purina Mainstay, 18% crude protein; per Jespersen and Toft 2003) until they successfully moulted to the second instar (7–10 days). Spiderlings reared from wild-collected females were randomly distributed among treatments in all experiments to minimize the potential for confounding maternal effects.

All experimental spiders were reared in individual Perspex containers (8 cm height × 4.5 cm diameter) screened with fine mesh on the top and equipped with a 1-cm-deep layer of sand that was kept semi-saturated to provide humidity. These microcosms were maintained at 21°C on a long day cycle (16:8 h) for the duration of each experiment. A plastic straw was placed vertically in the container to provide web attachment points. All spiders in experiments were fed adult *D. melanogaster* (average individual mass: 1.07 ± 0.02 mg).

Experiment 1. Food limitation effects on growth and mortality risk

Wild-collected juvenile spiders varying in initial size between 3.0 and 5.0 mm (first walking leg tibia + patella length or TPL) were used to test the hypotheses that growth rate is plastic and that rapid growth may carry inherent physiological costs for *T. versicolor*. Although this size range likely represents at least two separate instars, sufficient individuals within a single size class were not available. To minimize the effects of this size range within our experiment, we randomized the distribution of individuals between treatments, tested for differences in mean size by treatment at the start of the experiment, and used initial size as a covariate in our analyses.

Wild-collected spiders were held in individual containers until they moulted; spiders not moulting with 5 days of capture were not used in the experiment. Immediately following the moult individual spiders were randomly assigned to one of five food levels, calculated as a percentage of the average initial mass of a spider at the beginning of the experiment (Table 1). The experimental treatments ended after 40 days or when each individual moulted a second time. Immediately following the second moult (final for this experiment), TPL and mass were recorded (to the nearest 0.1 mm and 0.1 mg). Length of time between moults (intermoult period) or time to death were also recorded. The intermoult period for spiders dying during a moult was measured as the time to death or moribund state (hanging or fallen from web with no response to contact by the observer). Following Higgins and Rankin (2001), we calculated the change in mass as a percentage change per unit time:

$$\text{growth rate} = \left(\left(\frac{m_2}{m_1}\right)^{\frac{1}{t}} - 1\right)100$$

Using the maximum mass prior to the moult (t = intermoult duration in days) as the second measure of mass (m_2). Growth rates were $\ln(x + 1)$ transformed to successfully improve normality of ratio data. We used an analysis of covariance (ANCOVA) to assess the variation in growth rate between treatments with the initial mass (m_1) of spiders as the covariate. Since our assumption of homogeneous slopes was met, we removed the interaction between initial mass and growth rate from the model as recommended by Engqvist (2005). Differences in the length of the intermoult period between the five feeding levels were assessed using ANOVA. We used a χ^2-test and a 3 × 3 contingency table (PROC GENMOD in SAS version 9.0; SAS Institute, Cary, N.J.) to determine the effect of feeding rate on total mortality by treatment. The two lowest feeding levels and the two highest feeding levels were combined (treatments = low, medium, high) to minimize difficulties with small cell sizes. Spiders were scored as either alive, dead or dead during the moult. We confirmed that model assumptions were met using visual assessment of residuals and normal probability plots. We employed a Bonferroni correction to adjust our critical value for multiple non-independent tests.

Experiment 2. Compensatory growth

We conducted a laboratory experiment to test the ability of the long-jawed spider *T. versicolor* to catch up on growth following nutritional deficiency in the initial period of independent life. Once lab-reared spiderlings moulted to the second instar, they were randomly assigned to one of two treatments. Treatments were either a constant (C, $n = 11$) supply of two fruit flies per day for 28 days, or a switching treatment ($n = 11$) consisting of 14 days at one quarter of the food in the

Table 1 Treatment identifier, sample sizes, and number and mass of prey offered in experiment 1 to assess growth rate plasticity and mortality risk of rapid growth

Treatment	*n*	Number of prey offered (per day)	Mass of prey offered (mg/day)	Prey percent (daily rate) of average initial spider mass
I	9	0.25	0.27	1.9
II	9	0.5	0.54	3.8
III	10	1	1.07	7.6
IV	9	2	2.14	15.2
V	9	4	4.28	30.3

constant group (one fruit fly every second day) followed by 14 days at full food (Fig. 1a).

We measured the TPL and mass (mg) of all spiders on the first day of the experiment, on the day of the switch in food rations and at the conclusion of the experiment. To account for the effect of decreasing food amounts relative to body size, we calculated the natural log-transformed rate of growth between the starting mass and mass at the time of food ration switch (rate 1) and the natural log-transformed rate of growth between the time of food ration switch and the completion of the experiment (rate 2), and standardized both of these rates by the ration provided in each time step to produce the ration specific growth rates for each time period. We then combined these response variables in a multivariate ANOVA (MANOVA) design. We used separate ANOVAs for each time period as post hoc tests with a Bonferroni correction to adjust for multiple tests. Additionally, we tested whether differences in growth rates produced differences in final size using an ANCOVA with final mass (mg) as the response variable and initial mass as the covariate. Since our assumption of homogeneous slopes was met, we removed the interaction between initial and final mass from the model as recommended by Engqvist (2005). We used visual assessments of residual and normal probability plots to confirm that data met the assumptions of these models.

Experiment 3. Timing of subsidy resource and juvenile development

Early subsidy abundance may produce rapid growth, while later abundance (with early restriction in resources) can produce compensatory growth. Alternately, animals might experience a more constant environment. In order to determine which developmental path will produce the greatest payoff in terms of adult condition and fitness we tested the effect of these different subsidy schedules on measures of spider fitness. Food quantities were not scaled to increasing spider mass since we wished to test a scenario of shifting timing of an absolute quantity of food. The experiment was designed so that each spider received the same total amount (mg) of prey over the course of the experiment, regardless of which treatment it had been assigned. Our experiment tested differences in response to a large burst of food (relative to spider size) early in development against a smaller subsidy of food (again, smaller relative to spider size) close to the final moult to

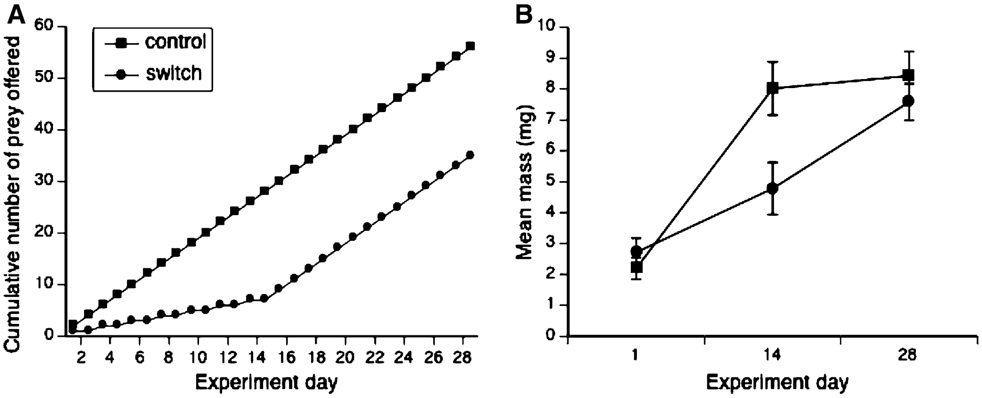

Fig. 1 **a** Cumulative number of prey offered at a constant rate of food supply (*control*) and a switching treatment (*switch*): initial food restriction followed by food supplied at the same rate as in the control treatment. **b** Mean mass of spiders (±1 SE) over a 28-day experiment, fed either a constant food supply (*control*) or a switching treatment consisting of 7 days of low food followed by 7 days of the same amount of food as received by individuals in the control treatment (*switch*). Overall growth rates do not differ while growth rates between the start of the experiment and day 7 and between day 7 and the end of the experiment, differ significantly between treatments

adulthood. These subsidy pulses were compared to a scenario of unvarying food supply. This lab scenario is a realistic abstraction of natural processes since abundances of emerging aquatic insects from the headwater streams where spiders were collected tend to exhibit multiple, relatively equal, peaks of emergence throughout the summer.

Lab-reared juveniles that had successfully moulted to the second instar were randomly assigned to one of three treatments: two variable or switching food levels and a constant "control". Animals assigned to the high:low (HL; $n = 24$) treatment received a large pulse of food for the first 7 days of the experiment and then a constant low rate of food. Animals in the low:high (LH, $n = 23$) treatment received a constant low rate of food until the penultimate week of the experiment when they received a 7-day pulse of high food. Animals in the C treatment ($n = 23$) received the same amount of food each day of the experiment. The length of the experiment (64 days) was selected to ensure that individuals in all three treatments received the same *total* number of prey over the course of the experiment and that only the timing of prey delivery was varied (Fig. 2a). The experimental treatments ended after 64 days or when each individual died.

Spiders that died before the completion of the experiment were eliminated from the growth analysis to avoid biasing overall growth rates. We recorded the length of time between moults (intermoult period) for each spider. Immediately following each moult, TPL (mm) and mass (mg) were measured. We fit second-order polynomial equations to the growth data for each spider and used the coefficients from these equations as response variables in a MANOVA to compare the shape of the growth functions for individual spiders by treatment (Meredith and Stehman 1991). This analysis of linear and quadratic coefficients directly addresses the shape of the response function. Differences between pairs of treatments were determined using MANOVAs for each possible pair of treatments with a Bonferroni correction for multiple non-independent tests. We compared the mean number of moults over the 64-day experiment using a single-factor ANOVA and an ANCOVA model to compare the final mass of spiders with treatment as the factor and initial size (TPL) as the covariate. For ANCOVAs, we tested for interactions between the main factor and the covariate and removed these interactions from models when they proved to be non-significant (Engqvist 2005). We used visual assessments of residual and normal probability plots to confirm that data met the assumptions of these models.

We developed a qualitative scale of reproductive development with four categories: no evidence of reproductive tissue (juvenile); minor sclerotization present or minor tissue swellings where gonads (males) or spermathecae (females) will develop (immature); presence of reproductive tissues obvious, but not yet complete (subadult); or male palps fully formed, female spermathecae present on dissection (adult). By the end of our 64-day experiment, only one individual had completed a final moult to maturity; since distinguishing between males and females is not possible for the juvenile stage we did not include sex in our analyses. The single adult male was excluded from analyses of body size and condition since male size:shape relationships change dramatically at the final moult—this individual represented a clear outlier in all exploratory analyses. We used a χ^2-test to determine differences in reproductive stage between treatments at the end of the experiment (PROC GENMOD in SAS). We assessed final condition using an ANCOVA with final TPL as the covariate, treatment as the main factor and final body size as the response variable (Garcia-Berthou 2001).

We used established biochemical assays (Allen 1976; Bligh 1959; Frings et al. 1972; Van Handel 1985) to measure the absolute quantity of glycogen, lipids, protein

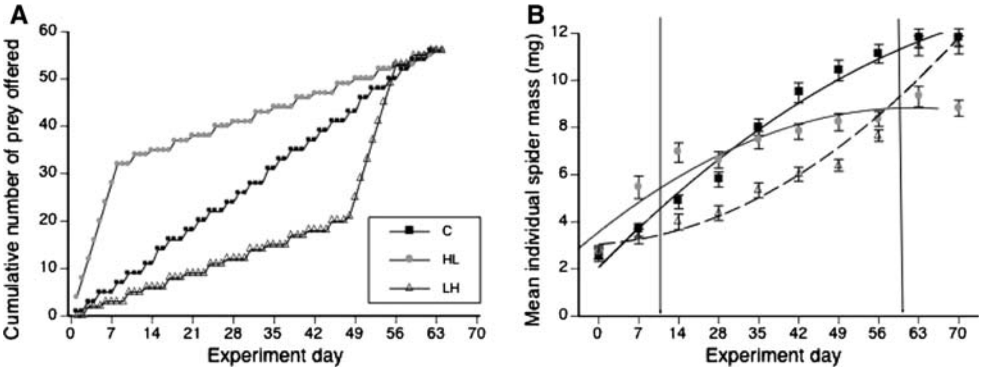

Fig. 2 **a** Cumulative number of prey offered in three treatments. Treatments were a constant level of food supply (*C*) and two switching treatments: initial high food followed by low food (*HL*) and initial low food followed by high food (*LH*). **b** Second-order polynomials fit to the mean mass (±1 SE) (mg) of spiders in three treatments over time. The *leftmost vertical line* indicates the time of switching for the HL treatment and the *rightmost vertical line* indicates the time of treatment switching for the LH treatment

and sugars present in individual spiders. Results from glycogen and sugar assays were determined by recording the colorimetric change in controls followed by samples at 625 nm; the optical density of lipid and protein assays were determined at 525 nm (Beckman DU 640 spectrophotometer; Beckman Coulter, Fullerton, CA, USA). Standard curves were generated to transform absorbance values into absolute amounts. We used a MANCOVA with the amount (µg) of each storage compound as multiple response variables and final body size as a covariate to explore differences in stored reserves between individual spiders in our treatments at the completion of the experiment. We used separate ANCOVAs for each body compound as post hoc tests to determine which body components were contributing to a significant overall effect in the MANCOVA design. Final body size was the covariate in these models. We employed a Bonferroni correction to adjust for multiple non-independent tests. Homogeneity of the regression lines and other assumptions required for MANCOVA were tested using standard procedures (Tabachnick and Fidell 2001).

Results

Experiment 1. Food limitation effects on growth and mortality risk

Growth and development in the spiders differed significantly between the five treatments. At the start of the experiment, there were no differences among the treatment groups in initial size (ANOVA, $F_{4,42} = 1.49$, $P = 0.22$). The rate of growth differed between treatments (ANCOVA, treatment, $F_{4,42} = 8.81$, $P < 0.001$; Fig. 3), increasing with increasing food rations (Fig. 3a). The model was significantly affected by the initial size (covariate) of the individual (ANCOVA, initial size, $F_{1,42} = 5.81$, $P = 0.02$). The interaction between initial size and treatment was not significant (ANCOVA, initial size by treatment, $F_{4,38} = 1.54$, $P = 0.21$) and was removed from the model prior to interpretation.

The length of the intermoult period tends to decrease with increasing food levels (ANOVA, treatment $F_{4,42} = 2.47$, $P = 0.059$; Fig. 3b). There was a significant effect of treatment on survival to the next instar (Pearson $\chi^2 = 23.34$, $P < 0.001$). Spiders in the two highest feeding regimes were significantly more likely to die during moulting than spiders in lower feeding regimes. In the two lowest feeding regimes, mortality was 78.9% while spiders in the middle feeding regime died at a rate of 80%. None of these deaths occurred during a moult. In contrast, 44.4% of spiders died in the two highest feeding regimes—of these deaths, 63% occurred during moulting (Fig. 3c).

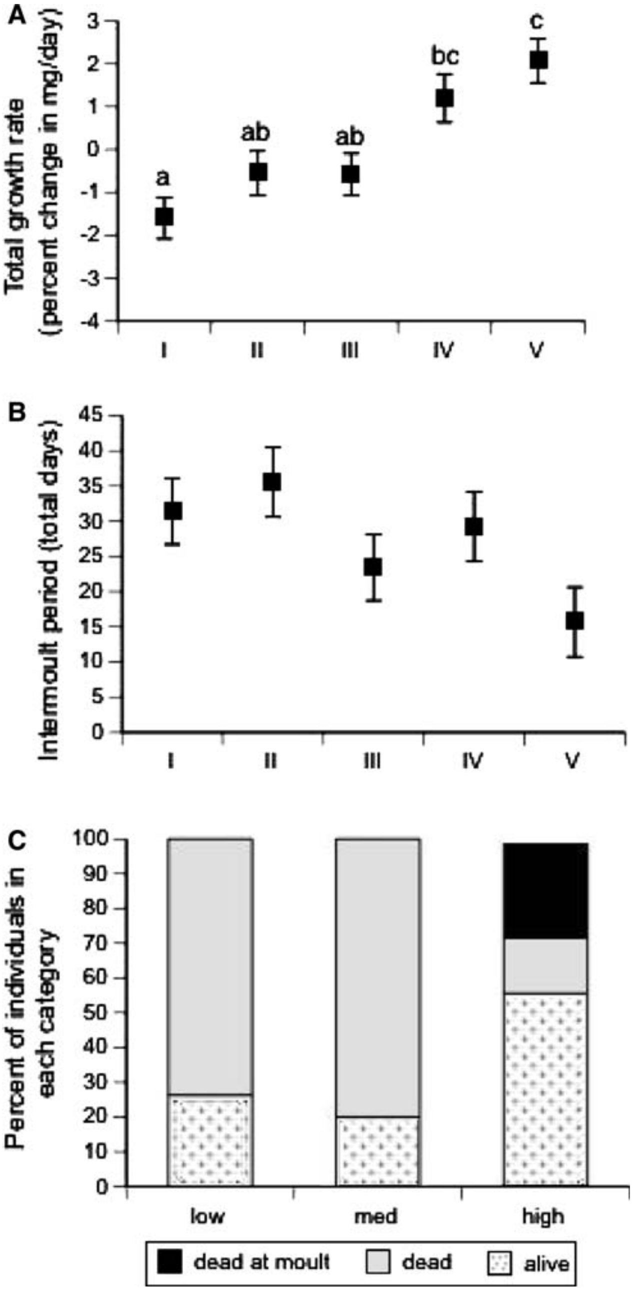

Fig. 3 **a** Mean total growth rates (percent change in mg/day) (±1 SE) for spiders in five treatments ranging from low (*I*) to high (*V*) levels of food availability. *Different letters* above a bar indicate significant differences for pairwise contrasts using a Bonferroni correction. **b** Mean period in days between initial moult and final moult in five treatments (I–V). **c** Percent of individuals that were alive, dead, or died during moulting in each of three treatment groups: *low* (pooled data from treatments I and II), medium (*med*; treatment III) and *high* (pooled data from treatments IV and V)

Experiment 2. Compensatory growth

There were no differences in initial distribution of masses (mg) between treatments (ANOVA, $F_{1,20} = 0.80$, $P = 0.381$). Overall growth rates between the two treatments differed significantly across both time periods (MANOVA, Wilks' exact λ $F_{2,19} = 18.29$, $P < 0.0001$). Post-hoc comparisons show that spiders in the switching treatment grew significantly slower relative to their ration during the first time period and significantly faster during the second time period than spiders with constant food conditions (Fig. 1b). There were no differences between the two treatments in the mass of spiders at the conclusion of the experiment (ANOVA, $F_{1,20} = 0.735$, $P = 0.402$).

Experiment 3. Timing of subsidy resource in juvenile development

Growth

There were no differences among the treatment groups in initial size ($F_{2,67} = 0.05$, $P = 0.95$, $n = 70$ individuals). The growth curves differed significantly between treatments (MANOVA, effect of treatment, Wilks' exact λ $F_{6,120} = 51.57$, $P < 0.001$; Fig. 2b). Both the linear (slope) and quadratic (curvature) terms differed between treatments (linear $F_{2,62} = 89.7$, $P < 0.001$, quadratic $F_{2,62} = 131.9$, $P < 0.001$). The overall rate of growth for spiders in the LH and C treatments did not differ (no difference in linear slopes, $P = 0.13$) while spiders in the HL treatment grew at an overall slower rate than spiders in the other two treatments ($\mathrm{LH} = \mathrm{C} > \mathrm{HL}$, $P < 0.001$). The curvature of each growth curve was significantly different for all contrasts (all $P < 0.05$). The final mass achieved by spiders differed between treatments (ANOVA, $F_{2,62} = 19.86$, $P < 0.0001$); spiders in the HL treatment were significantly lighter than spiders in the LH and C groups (Fig. 2b) at the conclusion of the experiment. Timing of food abundance altered the total number of moults per treatment (ANOVA, effect of treatment, $F_{2,62} = 3.13$, $P = 0.05$) with spiders in the HL completing fewer moults than spiders in either the LH or control treatments (Fig. 4a).

Reproductive stage and condition

Our analysis of the body condition of spiders at the completion of the experiment showed a significant effect of treatment and the covariate final TPL, but not their interaction which was removed from the model (ANCOVA, treatment, $F_{2,60} = 5.70$, $P = 0.005$; final TPL, $F_{1,60} = 81.87$, $P < 0.001$). HL were lighter for their size than animals in the constant food treatment (Fig. 4b). The relative composition of spider body components differed at the end of the experiment (MANCOVA, Wilks' λ exact $F_{8,110} = 2.89$, $P = 0.006$). Separate ANCOVAs for lipids, proteins, carbohydrates and glycogen showed that only lipids differed by treatment (effect of treatment $F_{2,57} = 4.32$, $P = 0.018$) with spiders in the LH treatment having greater amounts of lipids relative to their body size compared with animals in the HL treatment [mean mass-specific lipid content for spiders in treatment LH = 197.09 (±13.22) μg, HL = 118.52 (±14.22) μg and C = 183.45 (±13.86) μg]. Animals in the C treatment did not differ from the other treatments with respect to their lipid content once final body size was controlled for (Fig. 4c). Treatments differed according to the reproductive stage of spiders at the end of the experiment ($\chi^2 = 44.9$, $P < 0.001$). Animals receiving the LH switching treatment finished the experiment with more individuals in the penultimate moult before maturity (subadults) followed by HL and then C (Fig. 4d). In general, animals in the HL treatment were dominantly in the earliest reproductive category (juvenile) while more animals in the constant food treatment were immature (Fig. 4d).

Discussion

Our results suggest that spiders receiving large subsidies of food later in their development will reach reproductive capacity in the same or better condition, with the same or better stored resources, and get there faster relative to animals receiving either constant supplies of food or early resource pulses. Receiving large amounts of food early in life appears to actually confer disadvantages in terms of later performance—the physiological costs of early rapid growth appear greater in terms of fitness than whatever delayed costs of compensatory growth might be expressed later in life. Subsidies may thus provide greater benefits to individuals or age cohorts encountering this resource abundance immediately prior to reproductive efforts over subsidies arriving early in development.

Across a variety of taxa, researchers have demonstrated that the early restriction of food followed by a later switch to high food levels produces compensatory growth responses that may exceed the growth of individuals reared on constant high food amounts. This effect has been demonstrated for the larvae of amphibians (Beck 1997), and freshwater (Twombly 1996) and marine invertebrates (Hentschel and Emlet 2000). In our study we found support for both higher mortality rates during the moult with high juvenile growth rates and compensatory growth responses following food restriction. In our final experiment, when juvenile *T. versicolor* were exposed to large rations of food after a period of initial low food (mimicking the supply of aquatic prey subsidies), their overall response was a dramatic increase in body size, developmental stage and lipid storage. When individuals experienced low food following

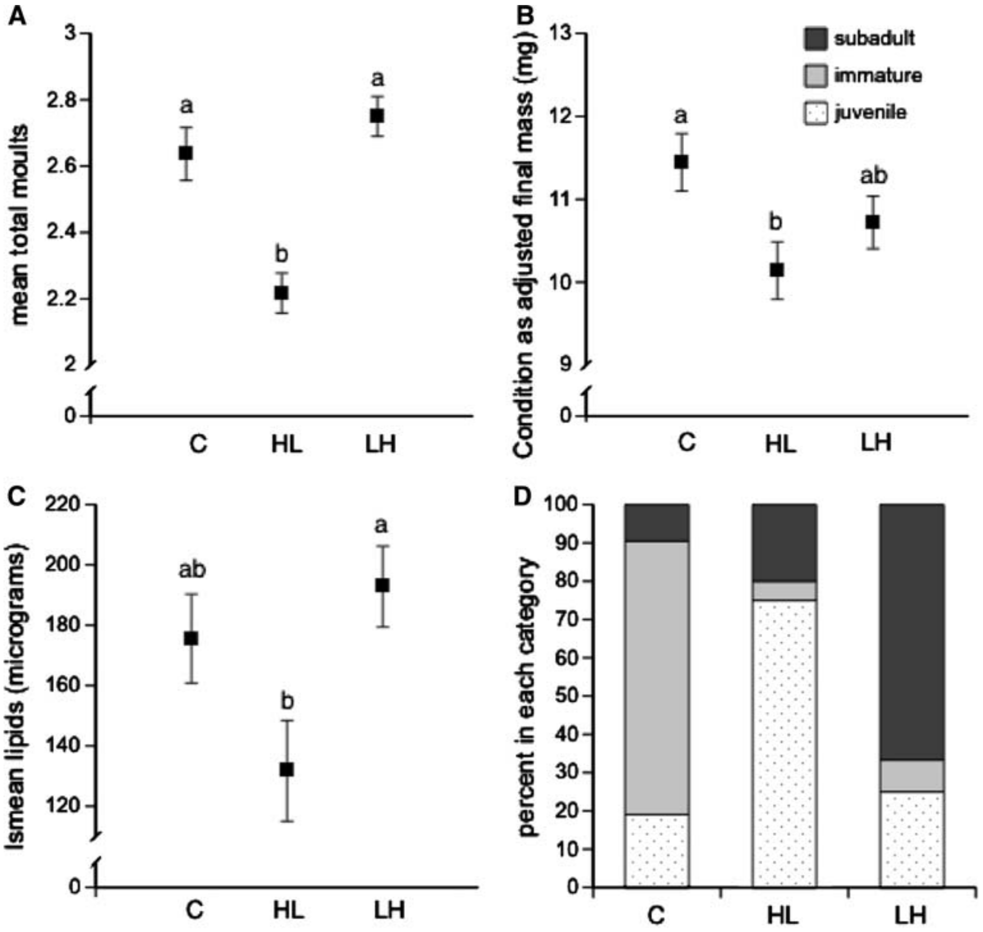

Fig. 4 **a** Mean number of moults completed per individual in each of three treatments (C, HL or LH). (See Fig. 2 or Materials and methods for abbreviations and description of treatments.) *Different letters* above a bar indicate significant differences using a Bonferroni correction. **b** Final mean mass (±1 SE) of spiders (adjusted for final size) fed three diets differing in timing of peak food availability. *Different letters* above a bar indicate significant differences using a Bonferroni correction. **c** Mean mass-specific lipid content per individual (±1 SE) for spiders fed three diets differing in timing of peak food availability. *Different letters* above a bar indicate significant differences in pairwise contrasts following a Bonferroni correction. **d** Percent of individual spiders assigned to each of three reproductive stages (immature, juvenile or subadult) based on presence and sclerotization of reproductive tissues in each of three diets differing in timing of peak food availability

an initial period of food abundance they experienced decreased growth, developmental stage and lipid storage relative to animals that received either a constant delivery of food or low food followed by a switch to high food. These results suggest that the timing of the brief availability of very abundant aquatic insects could play a significant role in the relative growth and development of riparian spiders between age classes or in populations in two habitat patches differing in their subsidy timing.

Costs of rapid growth and growth compensation

Although very high rates of growth might be assumed to increase fitness, allowing animals to avoid costs of slow development, or small size, there is a growing body of evidence supporting the existence of both extrinsic ecological and intrinsic physiological costs associated with rapidly increasing mass (Abrams et al. 1996; Higgins and Rankin 2001; Metcalfe and Monaghan 2001). The ecological costs of rapid growth include an increased risk of predation and parasitism associated with the presumed increased foraging necessary to fuel rapid gains in mass (Abrams et al. 1996). Physiological costs have been comparatively less well studied but include a decreased resistance to starvation or other environmental stresses (Stockoff 1991) or a decrease in other functions such as development (Arendt 1997).

In univoltine populations of *Nephila clavipes*, Higgins and Rankin (2001) found evidence for physiological costs of rapidly increasing mass. These results are corroborated here for *T. versicolor*. We found support for an increasing mortality risk for spiders fed very large numbers of prey. As in the study by Higgins and Rankin (2001) these deaths occurred during moulting. Potential explanations for the death of well-fed *T. versicolor* juveniles include gut failure following overeating, changes in the functioning or regulation of moulting hormones or nutritional imbalances. In both *N. clavipes* and *T. versicolor* the temporal link between the moult cycle and death suggests that very large increases in mass may interfere with the moulting process. Our results further show that *T. versicolor* is able to respond to short-term food deprivation with increased rates of growth relative to individuals kept on a constant ration.

Once recovery had begun, growth accelerated and remained high until the mass deficit had been regained. These spiders accomplished this catch-up growth on a lower total ration than provided to the control group (spiders in switching treatments received 37.5 mg of prey on average while spiders in the control treatment received a total of 59.9 mg). Spiders as a group demonstrate strong resistance to starvation through physical characters such as a heavily reticulated midgut and greatly expandable abdomen (Foelix 1996) that suggests they have a capacity to take advantage of food when it is periodically abundant. The ability for growth compensation may also have evolved from strong selection on spiders to synchronize their reproduction to a specific season.

Subsidy timing and proxy measures of spider fitness

In this study, individual *T. versicolor* receiving late subsidies of food following early food restriction did as well or better for all measures of fitness (same final size, same number of moults, same body condition, same quantity of lipid storage, but faster reproductive development) than animals receiving a constant supply of food. These animals did better for all of these measures than individuals that received a large subsidy of food early in their development and were then food restricted for the remainder of the experiment. One possible explanation for how this occurred includes the development of a more efficient metabolism under stress (Parsons 2004). Individuals that receive luxury rations in early development do not need to conserve energy and may use resources less efficiently than animals that initially developed on low food levels. Animals developing on low food rations may experience induced metabolic efficiency and be able to more efficiently use food received later in their development for rapid growth and swift reproductive development (Parsons 2004; Smith 1976).

As a laboratory study, these experiments represent a significant abstraction from processes operating in nature. Although spiders are generalist predators known to perform best on a mixed diet (Amalin et al. 1999; Nyffeler 1999; Toft 1999) we used a nutrient-enhanced, single-species diet in order to minimize sources of variation. To our knowledge, natural feeding rates for *T. versicolor* have not been determined. Wise (1979) observed median daytime natural feeding rates for two araneid species of similar size to *T. versicolor* that were equivalent to approximately three fruit flies (range = 0–21) per 24-h period. In our experiments, treatments were selected to work with survival parameters expressed on the artificial diet we used in the lab. Feeding rates in the lab were thus likely lower than those potentially experienced in nature. In addition, we did not make a quantitative evaluation of the proportion of prey offered that were actually consumed by individual spiders, relying on the observation that "excess" prey were not routinely detected. An alternative explanation for the patterns we observed could simply be that smaller, younger, spiders are able to consume less prey or require less prey for their growth. The poor performance of individuals in the HL treatment could thus be a simple outcome of a mismatch between the availability of prey in the (experimental) environment and the developmental stage of the consumer. Larger (older) spiders are physically capable of consuming more food and thus are in a better position to capitalize on sudden abundances of resources. Although the outcome is similar—subsidies received during juvenile stages are not as beneficial as sudden food abundance received during later stages—a physiological mechanism may not be necessary to explain this result.

Many authors have noted the effects of temporal variability in resource availability as a determining factor in the distribution, abundance and fitness of organisms. In this study, we illustrate that the way in which a temporally variable subsidy intersects with the life history of an organism may critically alter whether that pulse of allochthonous food is received as a subsidy. Individuals of *T. versicolor* that received an initial high pulse of food (mimicking a short emergence of aquatic insects) followed by constricted food rations, performed worse on all measures of fitness (growth rate, final size, development time, body condition, lipid storage) than spiders that either experienced initially low levels of food availability followed by a late pulse of food (mimicking a late emergence of aquatic insects) or a constant supply of food. Receiving large subsidies of food early in life appears to actually confer disadvantages for this species relative to a constant food supply or a subsidy late in development—illustrating that the physiological costs of rapid growth may be greater than the later costs associated with compensatory growth (Emlet and Sadro 2006; Johnsson and Bohlin 2005; Yearsley et al. 2004). The timing of exposure to a resource subsidy can thus determine whether a subsidy produces benefits for an organism or produces the paradoxical effect of negative consequences relative to conspecifics—the population-level consequences of this variable benefit due to subsidies within a population should be further investigated.

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